

Studies on the Feeding Behavior and Host Specificity of a Tropical Ectoparasitic Snail in the Genus *Odostomia* (Pyramidellidae)

by

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Abstract. Snails in the genus *Odostomia* Fleming, 1813, are common intertidal ectoparasites in Panama Bay, Republic of Panama, yet nothing is known about their feeding behavior or host specificity. Evidence is presented indicating that one species, *Odostomia* (*Chrysallida*) *communis* (C. B. Adams, 1852), predominantly parasitizes serpulid polychaete worms (Serpulidae). Like many North American and European pyramidellids, however, *O. communis* is not host specific and will also feed on several sympatric species of bivalves. A distinct searching behavior that may aid in locating hosts at a distance is described for these snails.

INTRODUCTION

Snails in the family Pyramidellidae are marine ectoparasites that feed on the body fluids of many invertebrates including polychaetes, gastropods, and bivalves (*e.g.*, FRETTER & GRAHAM, 1949a, b; ROBERTSON, 1957; ALLEN, 1958; ANKEL, 1959; SCHELTEMA, 1965; WELLS & WELLS, 1969; ROBERTSON & MAU-LASTOVICKA, 1979) and, in some cases, polyplacophorans and echinoderms (for a review see ROBERTSON & ORR, 1961). These ectoparasites have an eversible proboscis that can be attached to their hosts using an oral sucker located at the distal end. Once attached, the snail perforates the host's body wall with a pinlike stylet, and sucks blood and perhaps tissue debris by means of a buccal pump (FRETTER & GRAHAM, 1949b).

Early studies suggested that members of this family were host specific, parasitizing individuals of only one species (FRETTER & GRAHAM, 1949a, b, 1962). It is now recognized, however, that many pyramidellids are generalists, capable of feeding on a variety of hosts to some extent (ALLEN, 1958; ANKEL & CHRISTENSEN, 1963; BOSS & MERRILL, 1965; SCHELTEMA, 1965; BULLOCK & BOSS, 1971; ROBERTSON & MAU-LASTOVICKA, 1979). Although many pyramidellids are not strictly host specific, most have a preferred host, one that is parasitized the majority of the time (BOSS & MERRILL, 1965; ROBERTSON & MAU-LASTOVICKA, 1979). Primary and secondary hosts for many North American and European pyramidellids have been reported, along with the feeding and host-se-

lection behavior of these ectoparasites (*e.g.*, COLE, 1951; COLE & HANCOCK, 1955; LOOSANOFF, 1956; ALLEN, 1958; ANKEL, 1959; ROBERTSON & ORR, 1961; ANKEL & CHRISTENSEN, 1963; SCHELTEMA, 1965; BOSS & MERRILL, 1965; WELLS & WELLS, 1969; ROBERTSON & MAU-LASTOVICKA, 1979).

Although much literature pertains to North American and European pyramidellids, almost nothing is known about the feeding behavior and host specificity of tropical pyramidellids, especially in tropical west America. In the genus *Odostomia* Fleming, 1813, alone, about 100 species are described from the Panamic province. The degree of host preference and specificity for these tropical snails has yet to be worked out (KEEN, 1971). The need for research on west American pyramidellids is particularly important because the greatest concentration of pyramidellids appears to be in the Pacific Ocean (LASERON, 1959).

Many pyramidellids are highly motile, frequently moving on and off hosts, spending time on the substratum (ANKEL & CHRISTENSEN, 1963; SCHELTEMA, 1965; BOSS & MERRILL, 1965; WHITE *et al.*, 1984) and perhaps on non-host organisms (ROBERTSON & ORR, 1961; ROBERTSON & MAU-LASTOVICKA, 1979). Therefore, the mere presence of a pyramidellid on or with another invertebrate is not proof that the invertebrate in question is host to the pyramidellid (ROBERTSON & ORR, 1961). ROBERTSON & MAU-LASTOVICKA (1979) suggested that to establish a host-ectoparasite relationship between an invertebrate and a pyramidellid, investigators need to demonstrate a consistent association with organisms in the field and then to

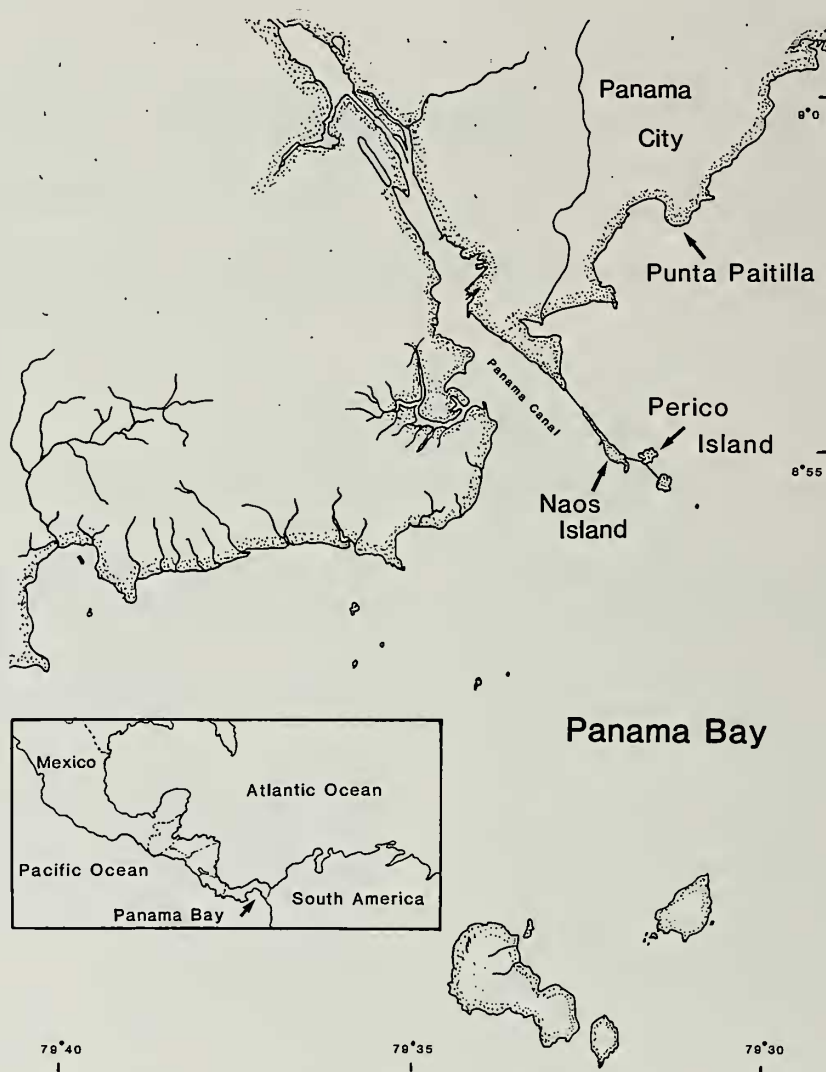


Figure 1

Study area in Panama Bay, Republic of Panama. Collections were made at Punta Paitilla and Perico Island.

determine whether these potential hosts are fed on in the laboratory. In this study, feeding behavior and host specificity of a tropical pyramidellid in the genus *Odostomia* were determined. Using field and laboratory observations and laboratory choice experiments I addressed the following questions: (1) Are these snails consistently associated with certain invertebrates in the field? (2) Which organisms will they feed on in the laboratory? (3) Which organisms are these snails attracted to in the laboratory? This research was conducted between September and December 1984, at the Smithsonian Tropical Research Institute, Naos Island laboratory, Panama City, Republic of Panama (08°55'N, 79°32'W).

MATERIALS AND METHODS

Field Investigations

Field observations and collecting were conducted at two similar sites in the rocky intertidal zone at Punta Paitilla and Perico Island in Panama Bay (Figure 1). Specimens of pyramidellids found within and around tidal pools were collected, and the two most abundant species sent to Mr. Miguel C. Aviles E. at the Department of Zoology, University of Panama, Republic of Panama. Mr. Aviles identified the larger snail as *Odostomia (Chrysallida) communis* (C. B. Adams, 1852) (Figure 2A) and the smaller snail as *Odostomia inconspicua* (C. B. Adams, 1852) (Figure 2B).

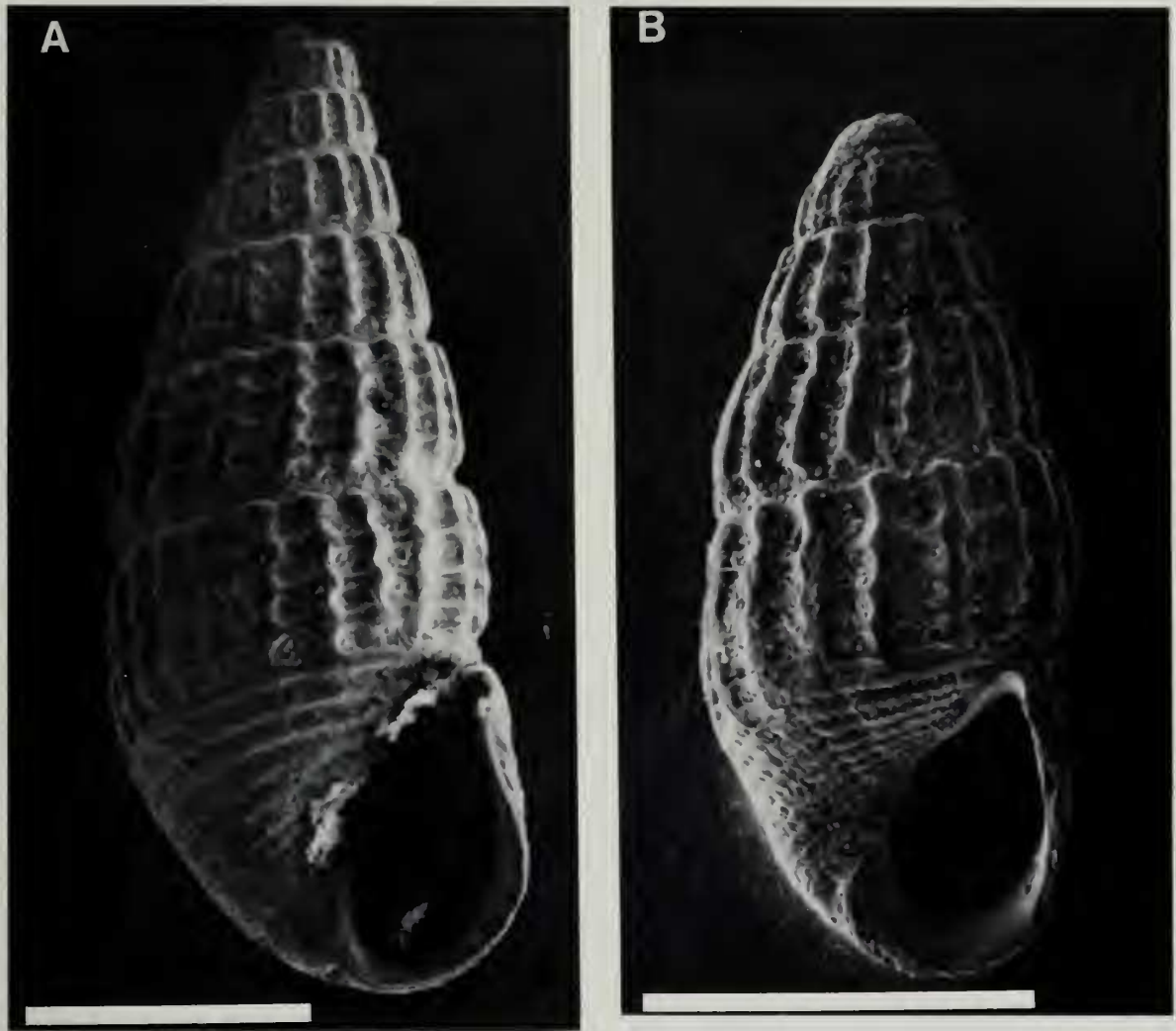


Figure 2

Scanning electron micrographs of ectoparasitic pyramidellids collected at Punta Paitilla and Perico Island, Panama Bay, Republic of Panama. Bars equal 1.0 mm. A. *Odostomia communis* (C. B. Adams, 1852). B. *Odostomia inconspicua* (C. B. Adams, 1852).

Representative samples of these snails are on deposit at the Academy of Natural Sciences of Philadelphia, Pennsylvania (ANSP A12637 and A10624A, respectively). Shell characteristics of these two species were also compared with the descriptions given by DALL & BARTSCH (1909), and were found to be consistent with those of *O. communis* and *O. inconspicua*. In addition, I collected several small (<1.0 mm) unidentified pyramidellids, and several individuals I identified as *Odostomia* (*Chrysallida*) *tyleri* Dall & Bartsch, 1909. All identifications were based on conchological characteristics, and therefore supraspecific designations should be considered tentative (ROBERTSON, 1978).

To determine with which organisms *Odostomia* spp. were

associated, I haphazardly collected a total of 48 rocks and shells of approximately the same size (10–20 cm) from tide pools at both sites. For each rock or shell (henceforth designated as sampled substrata) an estimate was made of the percentage of area in each of three categories: (1) area covered by serpulid polychaetes (all species), (2) area covered by other encrusting macroorganisms including sponges, bryozoans, non-motile gastropods, and bivalves, and (3) area not covered by any macroorganism. In addition, the number of *Odostomia* spp. associated with organisms in each of these categories was recorded. The criterion for association was established as the location of a snail within one shell height from a suspected host. This distance was easily within reach of the ectoparasite's proboscis, which

can be extended at least two times the shell height. In the field, it was difficult to distinguish species of *Odostomia*, owing to their small size (1–4 mm). Consequently, data are reported as the number of associated *Odostomia* spp., and represent snails in several species.

Data for the percentage of area covered by each of the three categories was scored from 0 to 10, with 10 being approximately 100% of the sampled substrata covered by a given category. A non-parametric Kruskal-Wallis test, followed by a non-parametric SNK procedure, was used to test for differences in the area covered by, and in numbers of *Odostomia* spp. associated with, each of the three categories. A non-parametric test was used because data were severely heteroscedastic and non-normal.

Indices of dispersion (I) were calculated for snails associated with each of the three categories using an s^2 to \bar{x} ratio. Pieces of sampled substrata were used as the sampling units ($n = 48$). The normal variable d was then calculated from I and compared to critical values (ELLIOTT, 1977).

Feeding Observations

Ectoparasites and organisms with which they were associated in the field were taken to the laboratory for further observations. Ten to 15 individuals of *Odostomia communis* were placed in a large finger-bowl filled with seawater (26–30°C) and offered suspected host organisms two or three species at a time, including: (1) serpulid polychaetes (several unidentified species), (2) *Isognomon recognitus* (Mabille, 1895) (Bivalvia), (3) *Arcopsis solida* (Sowerby, 1833) (Bivalvia), (4) *Chama echinata* Broderip, 1835 (Bivalvia), (5) *Ostrea palmula* Carpenter, 1857 (Bivalvia), (6) *Lithophaga aristata* (Dillwyn, 1817) (Bivalvia), (7) *Tellina* sp. (Bivalvia), (8) columbellid gastropod (Columbellidae), (9) vermetid gastropod (Vermetidae), (10) tunicates, (11) encrusting sponges, and (12) colonial bryozoans. Observations on the feeding behavior of *Odostomia communis* were made using a dissecting microscope over 8-h periods on nine different days.

Choice Experiments

Based on feeding observations of *Odostomia communis*, I selected five test organisms for choice experiments: (1) serpulid polychaetes, (2) *Isognomon recognitus*, (3) *Arcopsis solida*, (4) *Chama echinata*, and (5) *Ostrea palmula*. Test organisms were scrubbed to remove fouling material and weighed. Approximately equal weights of test organisms were used in each experiment; therefore, several individuals of the smaller species were used in order to obtain comparable live weights. All serpulids used in the experiments were encrusted onto small rocks and live weights were difficult to obtain. Consequently, 15–20 living serpulids of about the same size were used.

For each experiment, individuals of the five test organisms were placed in a large fingerbowl equidistant from the center and close to the sides of the bowl. The fingerbowl

was filled with seawater (26–30°C), and an airstone was suspended in the center of the bowl to provide mixing. Twenty-six to 30 starved (24 h) *Odostomia communis* were then placed in the center of the bowl below the airstone and allowed to move freely for 3 h. At the end of the experiment all test organisms were examined, and the number of snails associated with each organism (within 1 shell height) and number not associated with any organism were recorded.

Four replicate groups of snails were used (designated G1–G4). Each group was tested in three trials, on three consecutive days, using different test organisms each day. Two groups were tested per day. Between experiments the fingerbowl was scrubbed with fresh water and refilled with seawater. Test organisms were washed in fresh water and returned to the bowl. Their positions were haphazardly changed after each experiment to reduce effects of test-organism location on the snails' selection response.

Replicated goodness of fit tests (G -statistic) with William's correction were used to compare the observed distributions of *Odostomia communis* on the five test organisms in each trial with an expected 1:1:1:1:1 null distribution (SOKAL & ROHLF, 1981). In addition, for each trial, data for the four replicate groups were pooled and subdivided to determine which test organisms were responsible for any significant deviation from the null distribution ratio (ZAR, 1984). For all tests a significance level of $\alpha = 0.05$ was used.

RESULTS

Field Investigations

A total of 109 *Odostomia* spp. were examined in the field on 48 pieces of substrata. Of these, approximately 75.2% were associated with serpulid polychaetes, 5.5% were with other encrusting organisms, and 19.3% were not associated with any organism. The mean number of snails associated with serpulids was significantly higher than the number associated with other organisms, or those associated with no organism (non-parametric SNK, $P < 0.01$). An average of only $14.4 \pm 14.6\%$ (SD) of the area sampled, however, was covered by serpulid polychaetes, $22.5 \pm 19.3\%$ (SD) was covered by other encrusting organisms, and $65.7 \pm 26.0\%$ (SD) was free of encrusting organisms. The area covered by serpulids was significantly less than that covered by other organisms, or that which was free of encrusting organisms (SNK, $P < 0.01$).

For all sampled substrata, numbers of *Odostomia* spp. associated with serpulids, other organisms, and no organisms ranged from 0 to 9, 0 to 1, and 0 to 2, respectively. The index of dispersion (I) for snails associated with serpulids was 2.66, and was significantly different from unity ($d = 6.08$; $P < 0.01$), indicating a departure from a random distribution. Because d had a positive value and $s^2 > \bar{x}$, a contagious distribution was suspected. The indices of dispersion (I) for snails associated with other encrusting organisms, and with no organisms were 0.92 and 1.13, re-

spectively. These indices were not significantly different from unity ($d = -0.32$, other organisms; $d = 0.67$, no organism; $P > 0.05$), suggesting a random distribution.

Feeding Observations

Odostomia communis, like most pyramidellids, is a highly motile ectoparasite, frequently moving on and off host and non-host organisms. *Odostomia communis* exhibited three distinct behaviors in connection with host selection.

- (1) *Searching*—Snails repeatedly moving towards and away from potential hosts, rotating the shell left and right 180°. Repeatedly everting the proboscis and moving it across the substratum. In some instances perching on the posterior portion of the foot, with the head and tentacles lifted and the proboscis everted and waving back and forth above the head. This behavior usually was exhibited before contacting the soft parts of a potential host.
- (2) *Probing*—Snails stationary, the proboscis everted and moving, the oral sucker probing the soft body parts of a potential host.
- (3) *Feeding*—Snails stationary, the proboscis everted and the oral sucker gripping the soft body part of a host; buccal pumps vibrating.

Odostomia communis searched for, probed, and fed on serpulid worms most readily. Snails fed on serpulids by attaching their oral sucker to a bipinnate radiole of the worm. Extensive probing of the serpulid radioles usually occurred prior to attachment, and serpulids rarely displayed a strong withdrawal response when parasitic feeding began. Some snails were observed feeding from a single serpulid radiole for as long as 2 h. On several occasions juvenile *Odostomia* spp. (<1 mm in shell height) took up feeding positions on the operculum of serpulids, riding in and out of the calcareous tube when the serpulids retracted and expanded their crown of radioles.

Odostomia communis also searched for, probed, and fed on the bivalves *Isognomon recognitus* and *Arcopsis solida*. In addition, snails were observed searching for and probing the bivalves *Chama echinata* and *Ostrea palmula*; however, no feeding occurred. When searching a gaping bivalve, *Odostomia communis* often everted its proboscis many times along the left and right valve before it could locate the gape and probe the mantle tissue. This search for the mantle tissue of a bivalve took as long as 20 min. Snails were never observed searching for, probing, or feeding on the bivalves *Lithophaga aristata* and *Tellina* sp., or the columbellid and vermetid gastropods, or any tunicates, encrusting sponges, or bryozoans.

Choice Experiments

At the beginning of all experiments *Odostomia communis* moved out from the center of the bowl in all directions. None of the snails appeared to follow a conspecific mucus trail, and many exhibited the searching behavior described

earlier. At the end of 11 out of 12 experiments, the highest numbers of *Odostomia communis* were associated with serpulids (Table 1). In one experiment the highest number of snails, and in 5 out of 12 experiments the second highest numbers of snails, were found associated with *Ostrea palmula* (Table 1).

In all trials, the distribution of each of the four groups of *Odostomia communis* was significantly different from the expected even distribution (G -statistic, $P < 0.025$), and all four distributions were heterogeneous with respect to each other (G -statistic, $P < 0.05$). In addition, in each trial the pooled distribution of snails on all test organisms was significantly different from the null distribution (G -statistic, $P < 0.01$). Subdivided pooled distributions, however, indicated that on some test organisms an even distribution of snails did exist. In trials one and two, pooled distributions of snails on *Isognomon recognitus*, *Chama echinata*, and *Arcopsis solida* were not significantly different from the null distribution of 1:1:1 (G -statistic, $P > 0.25$), and in trial three, the pooled distribution of snails on all four bivalve species was not significantly different from the expected null distribution of 1:1:1:1 (G -statistic, $P > 0.25$).

DISCUSSION

Results indicate that *Odostomia communis* predominantly parasitizes serpulid polychaete worms. Like many North American and European pyramidellids, however, this tropical ectoparasite is not host specific and will also feed on two sympatric bivalves, *Isognomon recognitus* and *Arcopsis solida*. Several other pyramidellids, such as *Odostomia lukisii* Jeffreys, *Odostomia unidentata* (Montagu), *Odostomia plicata* (Montagu, 1803) (FRETTER & GRAHAM, 1949a; ANKEL, 1959), *Fargoa dianthophila* (Wells & Wells, 1961) (WELLS & WELLS, 1961; ROBERGE, 1968), and *Fargoa bartschi* (Winkley, 1909) (ROBERTSON, 1978), are known to parasitize serpulid worms.

In the field, the majority of *Odostomia* spp. individuals (75.2%) were consistently associated with serpulids, which covered the least amount of area ($\bar{x} = 14.4\%$). This is in contrast to the significantly fewer *Odostomia* spp. that were associated with other organisms (5.5%) and no organisms (19.3%), which covered significantly greater areas ($\bar{x} = 22.5\%$; $\bar{x} = 65.7\%$, respectively). In addition, the distribution of serpulid-associated snails was contagious. These data indicate that *Odostomia* spp. seek out and aggregate around serpulid polychaete worms. At least one other pyramidellid, *Boonea impressa* (Say, 1822), is contagiously distributed on its predominant host *Crassostrea virginica* (Gmelin, 1791) (WHITE *et al.*, 1984; POWELL *et al.*, 1987).

In choice experiments, *Odostomia communis* exhibited a clear preference for serpulid polychaetes over other organisms. In all trials, the highest total numbers of snails were consistently associated with serpulids (Table 1), and group and pooled distributions of snails on test organisms were significantly different from the expected even distri-

Table 1

Number of *Odostomia communis*, in each of the four groups, found associated with test organisms and with no organism at the end of choice-experiment trials. Each group was tested in three trials, on three consecutive days, using different test organisms each day. Groups G1 and G2, $n = 30$; groups G3 and G4, $n = 26$.

Found with	Numbers of associated ectoparasites														
	Trial 1					Trial 2					Trial 3				
	G1	G2	G3	G4	Total	G1	G2	G3	G4	Total	G1	G2	G3	G4	Total
Serpulid polychaetes	9	18	16	13	56	17	16	12	10	55	13	20	15	10	58
<i>Ostrea palmula</i>	11	10	0	4	25	5	2	1	9	17	7	2	2	1	12
<i>Isognomon recognitus</i>	3	0	1	4	8	2	1	0	2	5	0	1	6	4	11
<i>Chama echinata</i>	1	1	2	0	4	3	4	0	1	8	3	1	1	5	10
<i>Arcopsis solida</i>	2	0	1	1	4	1	0	2	0	3	2	2	0	1	5
No organism	4	1	6	4	15	2	7	11	4	24	5	4	2	5	16

bution. Subdivided pooled distributions indicate that the higher numbers of snails on serpulids and *Ostrea palmula* in trials one and two, and the higher numbers on serpulids in trial three, were responsible for the significant deviation from the null distribution. Interestingly, in one experiment the highest number, and in 5 out of 12 experiments the second highest numbers, of snails were associated with *Ostrea palmula* (Table 1); however, snails were never observed feeding on this bivalve, although extensive probing did occur. This finding emphasizes the concerns raised by ROBERTSON & ORR (1961) and ROBERTSON & MAU-LASTOVICKA (1979), that the presence of a pyramidellid with another invertebrate is not sufficient proof that a host-ectoparasite relationship exists.

Probing and feeding behaviors of *Odostomia communis* were similar to those reported for other pyramidellids (FRETTER & GRAHAM, 1949b, 1962; WELLS & WELLS, 1961). However, the searching behavior, of perching on the posterior portion of the foot with the head and tentacles lifted and the proboscis everted above the head, has not been previously reported. This behavior may be a response to dissolved chemicals given off by hosts, and along with rotating 180°, could aid in locating hosts at a distance. Chemoreception is ubiquitous in marine gastropods and is important in numerous interactions, including arousal and orientation to food (as reviewed by KOHN, 1983). The results of this research, as well as several aspects of the biology of pyramidellids such as the reduced osphradium, the highly developed tentacles (FRETTER & GRAHAM, 1949b), and motile behavior, suggest that these snails are adapted for chemolocation of hosts. As *Odostomia communis* moves closer to an organism, the proboscis is repeatedly everted and moved back and forth across the substratum; this behavior could increase the snail's chance of contacting a potential host.

Searching and probing by *Odostomia communis* usually led to feeding, especially when a serpulid host was selected. When a bivalve was selected, however, snails would frequently begin probing, but then stop and abandon their

host before any feeding was observed. This occurred most often when *Chama echinata* or *Ostrea palmula* were selected. In addition, snails spent more time searching for the soft parts of bivalves than for the soft parts of serpulids. *Odostomia communis* appeared to have difficulty finding the gape and contacting the mantle tissue of bivalves. Even after parasitic feeding began, if disturbed, snails could not relocate the bivalve's gape without everting their proboscises several times in an apparently haphazard fashion. Another pyramidellid, *Boonea impressa*, which is ectoparasitic predominantly on the oyster *Crassostrea virginica*, was never observed to exhibit this haphazard search for the mantle tissue of its host (WARD, 1985). These observations imply that *Odostomia communis* is less proficient at feeding on bivalves than on serpulids.

In conclusion, the predominant and preferred hosts of *Odostomia communis* are serpulid polychaete worms; however, these snails are not host specific and will also feed on several sympatric bivalves. *Odostomia communis* exhibits a distinct searching behavior that could aid in locating hosts at a distance, and searching and probing behaviors precede and usually lead to feeding. Future research should continue to include field observations, choice experiments, and direct observations of feeding to determine host preferences of tropical pyramidellid snails. In addition, research on the physiological mechanisms and chemicals involved in chemoreception is needed to determine how pyramidellids locate their varied hosts.

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LITERATURE CITED

- ALLEN, J. F. 1958. Feeding habits of two species of *Odostomia*. *Nautilus* 72:11-15.
- ANKEL, W. E. 1959. Beobachtungen an Pyramidelliden des Gullmar-Fjordes. *Zool. Anz.* 162:1-21.
- ANKEL, F. & A. M. CHRISTENSEN. 1963. Non-specificity in host selection by *Odostomia scalaris* Macgillivray. *Vidensk. Medd. fra Dansk Naturh. Foren.* 125:21-325.
- BOSS, K. J. & A. MERRILL. 1965. Degree of host specificity in two species of *Odostomia*. *Proc. Malacol. Soc. London* 36: 349-355.
- BULLOCK, R. C. & K. J. BOSS. 1971. Non-specificity of host-selection in the ectoparasitic snail *Odostomia* (*Menestho*) *bisuturalis* (Say) (Gastropoda: Pyramidellidae). *Breviora* 363: 1-7.
- COLE, H. A. 1951. An *Odostomia* attacking oysters. *Nature* 168: 953-954.
- COLE, H. A. & D. A. HANCOCK. 1955. *Odostomia* as a pest of oysters and mussels. *Jour. Mar. Biol. Assoc. U.K.* 34:25-31.
- DALL, W. H. & P. BARTSCH. 1909. A monograph of west American pyramidellid mollusks. *Bull. U.S. Natl. Mus.* 68: 1-258.
- ELLIOTT, J. M. 1977. Statistical analysis of samples of benthic invertebrates. 2nd ed. *Freshwater Biol. Assoc., Sci. Publ.*, No. 25:156 pp. Ambleside, U.K.
- FRETTER, V. & A. GRAHAM. 1949a. Feeding and reproduction in the pyramidellids. *Nature* 163:361-362.
- FRETTER, V. & A. GRAHAM. 1949b. The structure and mode of life of the Pyramidellidae, parasitic opisthobranchs. *Jour. Mar. Biol. Assoc. U.K.* 28:493-532.
- FRETTER, V. & A. GRAHAM. 1962. *British prosobranch molluscs*. Bartholomew Press: Dorking, U.K. 755 pp.
- KEEN, A. M. 1971. Sea shells of tropical west America. 2nd ed. Stanford Univ. Press: Stanford, Calif. 1064 pp.
- KOHN, A. J. 1983. Feeding biology of gastropods. Pp. 1-63. *In*: A. S. M. Saleuddin & K. M. Wilbur (eds.), *The Mollusca*. Vol. V. Physiology, part 2. Academic Press: New York, N.Y.
- LASERON, C. F. 1959. The family Pyramidellidae (Mollusca) from Northern Australia. *Australian Jour. Mar. Freshwat. Res.* 10:177-252.
- LOOSANOFF, V. L. 1956. Two obscure oyster enemies in New England waters. *Science* 123:1119-1120.
- POWELL, E. N., M. E. WHITE, E. A. WILSON & S. M. RAY. 1987. Small-scale spatial distribution of a pyramidellid snail ectoparasite, *Boonea impressa*, in relation to its host, *Crassostrea virginica*, on oyster reefs. *Mar. Ecol.* 8:107-130.
- ROBERGE, A. G. 1968. *Odostomia dianthophila* (Gastropoda, Pyramidellidae) from Buzzard's Bay, Mass., a north range extension. *Nautilus* 81:iii.
- ROBERTSON, R. 1957. Gastropod host of an *Odostomia*. *Nautilus* 70:96-97.
- ROBERTSON, R. 1978. Spermatophores of six eastern North American pyramidellid gastropods and their systematic significance (with the new genus *Boonea*). *Biol. Bull.* 155:360-382.
- ROBERTSON, R. & T. MAU-LASTOVICKA. 1979. The ectoparasitism of *Boonea* and *Fargoa* (Gastropoda: Pyramidellidae). *Biol. Bull.* 157:320-333.
- ROBERTSON, R. & V. ORR. 1961. Review of pyramidellid hosts, with notes on an *Odostomia* parasitic on a chiton. *Nautilus* 74:85-91.
- SCHELTEMA, A. H. 1965. Two gastropod hosts of the pyramidellid gastropod *Odostomia bisuturalis*. *Nautilus* 79:7-10.
- SOKAL, R. R. & F. J. ROHLF. 1981. *Biometry*. 2nd ed. W. H. Freeman and Co.: San Francisco, Calif. 859 pp.
- WARD, J. E. 1985. Effects of the ectoparasite *Boonea* (= *Odostomia*) *impressa* (Gastropoda: Pyramidellidae) on the growth rate, filtration rate, and valve movements of the host *Crassostrea virginica*. M.Sc. Thesis, Univ. of Delaware, College of Marine Studies, Lewes, Delaware.
- WELLS, H. W. & M. J. WELLS. 1961. Three species of *Odostomia* from North Carolina, with description of new species. *Nautilus* 74:149-157.
- WELLS, H. W. & M. J. WELLS. 1969. New host and distribution records of *Odostomia dianthophila*. *Nautilus* 82:109-110.
- WHITE, M. E., E. N. POWELL & C. L. KITTING. 1984. The ectoparasitic gastropod *Boonea* (= *Odostomia*) *impressa*: population ecology and the influence of parasitism on oyster growth rates. *Mar. Ecol.* 5:283-299.
- ZAR, J. H. 1984. *Biostatistical analysis*. Prentice-Hall Inc.: New Jersey. 718 pp.